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A new species of *Cardioglossa* (Amphibia: Anura: Arthroleptidae) endemic to Mount Manengouba in the Republic of Cameroon, with an analysis of morphological diversity in the genus

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A new frog species of the genus *Cardioglossa*, that is probably restricted to less than 10 km^2 of gallery forest near the summit of Mount Manengouba in the Republic of Cameroon, is described. Unlike all other *Cardioglossa*, in life the coloration of the new species is typically brownish red, with no dorsal markings, but with a pair of thin, golden white lines that extend posteriorly from the tip of the rostrum and terminate just above and behind the tympanum. This new species is morphologically similar to *C. oreas*, another high-altitude species endemic to the Cameroonian mountains: both have small tympana and lack the hypertrophied third manual digit typical of males of other *Cardioglossa*. The tadpole of the new species is similar to that of *C. occidentalis*, the only other *Cardioglossa* for which the tadpole is fully described, but differs in having a broad anterolaterally projecting supraoral labium, lacking ventral pigmentation, and having a relatively longer spiracular tube. Several features of tadpole morphology are convergent with the unusual fossorial tadpole of the microhylid *Otophryne* and suggest a similar convergence in ecology. Principal components analysis of morphometric data, followed by discriminant function analysis, was used to explore patterns of morphological similarity within *Cardioglossa*. These analyses provide support for five species groups: (1) *C. aureoli* (distinct from other *Cardioglossa*); (2) *C. escalerae*, *C. gratiosa* and *C. nigromaculata*; (3) *C. gracilis*, *C. melanogaster* and *C. schioetzi*; (4) **C. sp. nov.** and *C. oreas*; and (5) *C. cyaneospila*, *C. pulchra*, *C. venusta* and *C. trifasciata*. The inclusion of *C. cyaneospila* in the last group supports previous suggestions of past biotic connections between the Albertine Rift mountains and those of the Cameroon Volcanic Line. The description of this new species further emphasizes Mt Manengouba as a centre of anuran endemism within the Cameroonian mountains and reaffirms the importance of this ecoregion within sub-Saharan Africa.

ADDITIONAL KEYWORDS: Afromontane – Cameroon Volcanic Line – Central Africa – convergence – frog – morphometrics – tadpole – West Africa.

INTRODUCTION

The arthroleptid genus *Cardioglossa* currently comprises 16 species of terrestrial frogs found in tropical sub-Saharan Africa. Most of the diversity of this genus occurs in the Lower Guinean Forest Zone, with seven species (*C. alsco*, *C. melanogaster*, *C. oreas*, *C. pulchra*, *C. schioetzi*, *C. trifasciata* and *C. venusta*) found only in the highlands of Cameroon and Nigeria (Amiet, 1972a, 1981; Gartshore, 1986; Herrmann *et al*., 2004) and two other species (*C. gratiosa* and *C. nigromaculata*) found in low-elevation forests that extend from Cameroon into Nigeria, Equatorial Guinea and Gabon (Amiet, 1972a; Burger *et al*., 2006). Four additional lowland species (*C. elegans*, *C. escalerae*, *C. gracilis* and *C. leucomystax*) are more widespread and extend east and further south into the forests of the Congo River basin (Witte, 1934;

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Laurent, 1972; Joger, 1990; Largen & Dowsett-Lemaire, 1991; de la Riva, 1994). *Cardioglossa* also are known from other areas in Africa, including one species (*C. cyaneospila*) from the Albertine Rift mountains of Burundi, Rwanda and eastern Democratic Republic of Congo (Laurent, 1950) and two species (*C. aureoli* and *C. occidentalis*) known only from the Upper Guinean Forest Zone of West Africa (Schiøtz, 1964; Blackburn *et al*., in press).

The Upper and Lower Guinean Forest Zones and the Albertine Rift mountains are important centres of African biodiversity. All are likely locations of forested refugia during periods of the Pleistocene in which sub-Saharan Africa was significantly more arid than today (e.g. Moreau, 1966; Pomeroy, 1993; Fjeldså & Lovett, 1997; Linder, 2001; Brooks *et al*., 2002; Jetz & Rahbek, 2002). The ecoregion comprising the mountains of Cameroon, especially Mount Manengouba and other nearby mountains (Kupe, Nlonako, Bakossi, Rumphi), is one such refugium in which the environment has probably been stable over thousands, if not millions, of years (e.g. Fjeldså & Lovett, 1997; Maley *et al*., 1991). The Cameroonian mountain ecoregion is one of the most important in Africa in terms of both species richness and endemism and is also one of the most threatened ecoregions on the continent (Burgess *et al*., 2004). These mountains, comprising a large portion of the geological formation referred to as the Cameroon Volcanic Line, harbour a remarkable amount of biodiversity for many taxa including both plants (e.g. Lovett & Taplin, 2004) and vertebrates (e.g. Moreau, 1966; Amiet, 1975; Stuart, 1986a; Lawson, 1993; Herrmann *et al*., 2004, 2005a, b) and are part of the West African biodiversity hotspot defined by Myers *et al*. (2000). However, the processes leading to this diversity are still poorly understood (e.g. Amiet, 1987; Fjeldså & Lovett, 1997; Graham, Smith & Languy, 2005). Here I describe adults and tadpoles of a new species of *Cardioglossa* known only from Mt Manengouba, a large volcanic massif in the south-western region of the Cameroon Volcanic Line. This is the fourth anuran species that is strictly endemic to this mountain. This discovery further highlights Cameroon as a centre of anuran diversity in sub-Saharan Africa.

Developing a better understanding of the systematics of *Cardioglossa* may shed light on the spatial and temporal patterns of diversification of other African organisms. This is especially true for taxa with high diversity in the Cameroonian Volcanic Line and other Central African mountains. Unfortunately, as for many African taxa, samples of several species are unavailable for molecular analyses. To this end, the present study uses morphometric data to begin to understand patterns of diversity within *Cardioglossa*. I utilized a principal components analysis of morphometric data as an ordination technique to explore interspecific patterns of morphological diversity. A discriminant function analysis was conducted to assess the ability of morphometric data to discriminate species groups proposed in the literature as well as those patterns of similarity observed through principal components analysis. The observed patterns of interspecific morphological similarity presented here allow for inferences of species groups within *Cardioglossa* that can be tested using phylogenetic methods.

MATERIAL AND METHODS

Specimens of the both the new species and previously described *Cardioglossa* species were found during visual encounter surveys supplemented by searching under logs, leaves and rocks. Specimens were killed in an aqueous solution of chloretone and preserved in 10% neutral-buffered formalin. Before preservation, tissue samples from the liver of adults and tail musculature of tadpoles were taken and preserved in 95% ethanol. Specimens of every *Cardioglossa* species except *C. alsco* were examined during the course of this study (see Appendix 2). Coordinates are referenced to the WGS84 datum. Institutional abbreviations are as listed in Leviton *et al*. (1985).

Tadpoles collected at the type locality were linked to adults of the same species by using DNA sequence data. A continuous stretch of 2347 base pairs comprising the mitochondrial 12S and 16S ribosomal RNA genes and the intervening transfer RNA for valine was amplified using PCR and the primer pairs reported in Darst & Cannatella (2004). PCR products were purified using the Wizard Purification System (Promega), sequenced using BigDye v.3.1 (ABI) on an ABI 3730 sequencer, aligned using the default parameters in ClustalX v.1.83.1, and the amount of sequence divergence calculated between specimens. The GenBank accession numbers for the adult (MCZ A-136933) and tadpole (MCZ A-138157) are EU072196 and EU072197, respectively.

Measurements were taken to the nearest 0.1 mm under a dissecting microscope using digital calipers and followed the methodology of Blackburn (2005). Images of preserved specimens were obtained with a JVC 3-CCD digital camera mounted on a dissecting microscope using AutoMontage Pro 5.0 (Synoptics). Observations of skeletal morphology were made by digital radiographic analysis using a Thermo Kevex digital X-ray (Model PXS10) in combination with a PaxScan amorphous silicon sensor array (Model 4030R) and ViVa version 2.0 (Varian Medical Systems, Inc.); tadpoles were X-rayed at 30 kV and adult frogs at 40 kV. The brightness and contrast of images were adjusted using Photoshop version 7.0 (Adobe).

Morphometric analysis

I quantified 18 morphological characters of 110 *Cardioglossa* specimens that represent 15 of the 16 previously described species, including the type specimens of 12 species. These characters were chosen to capture differences in head shape and relative proportions of limb elements, which may be ecologically significant. Only adult specimens identified as males or females were included in the principal components analysis ($N = 88$). Males were determined to be mature by the presence of an elongate third manual digit and/or the presence of spines on the manual digits; females were determined either by the presence of ova or by having body sizes approximately equal to or larger than mature males. Five morphological characters describing the forelimb were excluded because these exhibited obvious sexual dimorphism (my unpublished observations). Females of many anuran species are larger than males, and thus nearly any measurement will differ between males and females; tests of sexual dimorphism for each species in this analysis are not possible because seven of the 17 species are represented only by males. The exclusion of the five measurements of the forelimb helps to ensure that comparisons between taxa are based on interspecific differences. Including males and females in a single analysis may obscure finer patterns that could emerge from analysing each sex separately. However, it also means that the patterns that emerge from an analysis pooling data from both sexes, which will thus increase the variance for each species, will be more robust and not contingent on including data from only one sex.

All data were natural log-transformed prior to analysis in order to acheive normalization. Statistical analyses were conducted using SPSS 13.0 for Mac OS X (SPSS Inc., Chicago, IL, USA) and significance was assessed based on $\alpha = 0.05$. Principal component analysis (PCA) was used to understand patterns of variation and covariation within the morphometric data. Component axes were scaled to be equal to their eigenvalues. PCA was performed using the covariance matrix, rather than a correlation matrix, in order to retain all information about variance and covariance. Those components accounting for 85% of the cumulative variance were examined and principal component (PC) scores were plotted in order to identify the relationship of species or species groups in morphospace. In those cases in which species or species groups appeared to differ in their scores for a particular PC axis, differences in component scores were analysed using a one-way analysis of variance (ANOVA). Discriminant function analysis (DFA) was then used to test patterns of interspecific similarity found both through PCA and proposed in the literature by Amiet (1981). The morphometric variables were treated as independent variables and a multivariate equation (function) was defined such that these groups were maximally discriminated. The model used for DFA was produced by a stepwise procedure in which the probability to stay in the model was $\alpha = 0.05$ and to be removed was $\alpha = 0.10$. Support for the interspecific patterns tested was evaluated based on the value of Wilks' λ for the discriminant functions and the ability of the model to classify the species groups correctly.

RESULTS

Cardioglossa manengouba sp. nov.

Figures 1–5, Table 1

Holotype: MCZ A-137909, adult male, Republic of Cameroon, Littoral Province, Mt Manengouba, 05°00′38.9″N, 09°51′24.8″E, montane gallery forest, approximately 2160 m elevation, 21.vii.2006, D.C. Blackburn, K.S. Blackburn, and M.T. Kouete.

Paratypes: MCZ A-136933, subadult male, same locality as holotype, 27.ix.2004, D.C. Blackburn, J.L. Diffo, and L.N. Gonwouo; MCZ A-137908, adult male, Southwest Province, Mt Manengouba, 05°01′48.9″N, 09°50′37.3″E, montane gallery forest, approximately 2190 m elevation, 21.vii.2006, D.C. Blackburn, K.S. Blackburn, and M.T. Kouete; MCZ A-138155-56, tadpoles, same collection data as MCZ A-137908; MCZ A-137910, adult female, same collection data as holotype; MCZ A-138153-54, A-138157-59, tadpoles, same locality data as MCZ A137909-10.

Diagnosis: Cardioglossa manengouba is of similar body size to most other Cameroonian *Cardioglossa*, with a broad head similar to *C. oreas* and *C. pulchra*. It is easily distinguishable from all other *Cardioglossa* by a pair of golden white lines that extend posteriorly from the tip of the rostrum along the canthus rostralis and the lateral edge of the upper eyelid, and terminate above and just posterior to the tympanum (Fig. 2B). These are the only prominent markings found on this species. *Cardioglossa manengouba* lacks both an infratympanal line and the three dorsal markings (i.e. cephalic, scapular and lumbar; Amiet, 1972a) typical of many *Cardioglossa* species. In life, the base coloration varies from ruddy brown to brownish red. There are no markings on the dorsum and few, if any, on the hindlimbs. There are often small golden markings on the lateral surface of the arm just above the elbow. Similar to *C. oreas*, males do not have a hypertrophied third manual digit (Fig. 3B). However, unlike *C. oreas*, the tympanum, while small, is distinct and males exhibit more pronounced spines on the second and third manual digits.

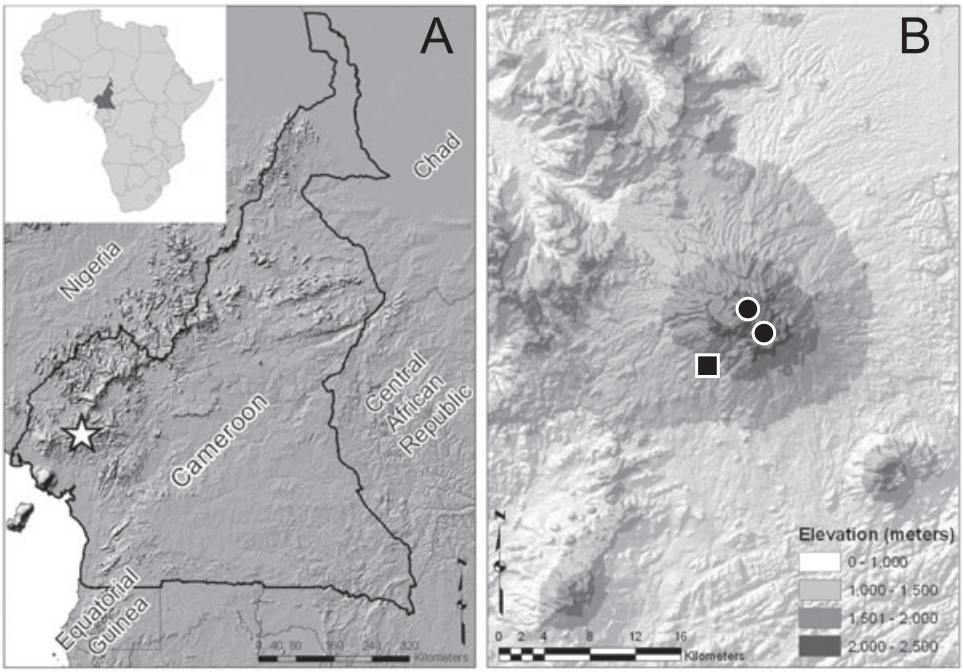

Figure 1. A, map showing topography of Cameroon and neighbouring countries. Inset shows position of Cameroon within Africa. White star indicates position of Mount Manengouba. B, topographic map of Mt Manengouba showing the two known localities (black circles) of ***Cardioglossa manengouba*** **sp. nov.** Nsoung, a commonly visited collecting locality, is included for reference (black square).

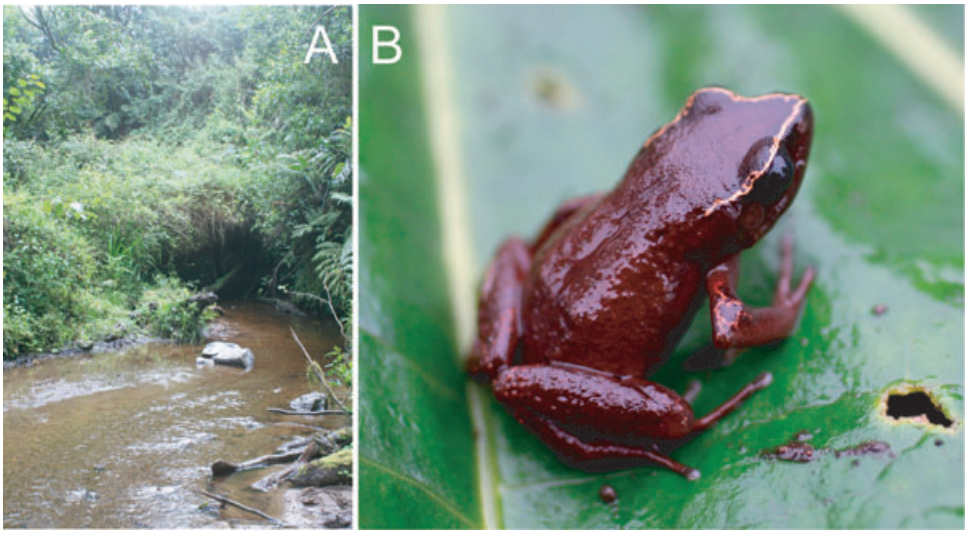

Figure 2. A, type locality of ***Cardioglossa manengouba*** **sp. nov.** in the montane forests of Mount Manengouba (approximately 2100 m above sea level). B, photograph of male paratype (MCZ A-137908) of *C. manengouba* in life.

Description of holotype: Adult male, SVL 23.0 mm (Fig. 3; Table 1). Medium-sized frog with slender limbs; head approximately wide as long; distance from naris to rostral tip less than that from naris to anterior eye; canthus rostralis rounded; distinct tympanum opaque, round and small; region behind tympanum slightly swollen and anterior margin marked by supratympanic fold; no premaxillary, maxillary or vomerine teeth; tongue without prominent median papilla and widens towards distal, free end.

Relative length of fingers: III > IV > II > I; two white and small, but prominent, palmar tubercles;

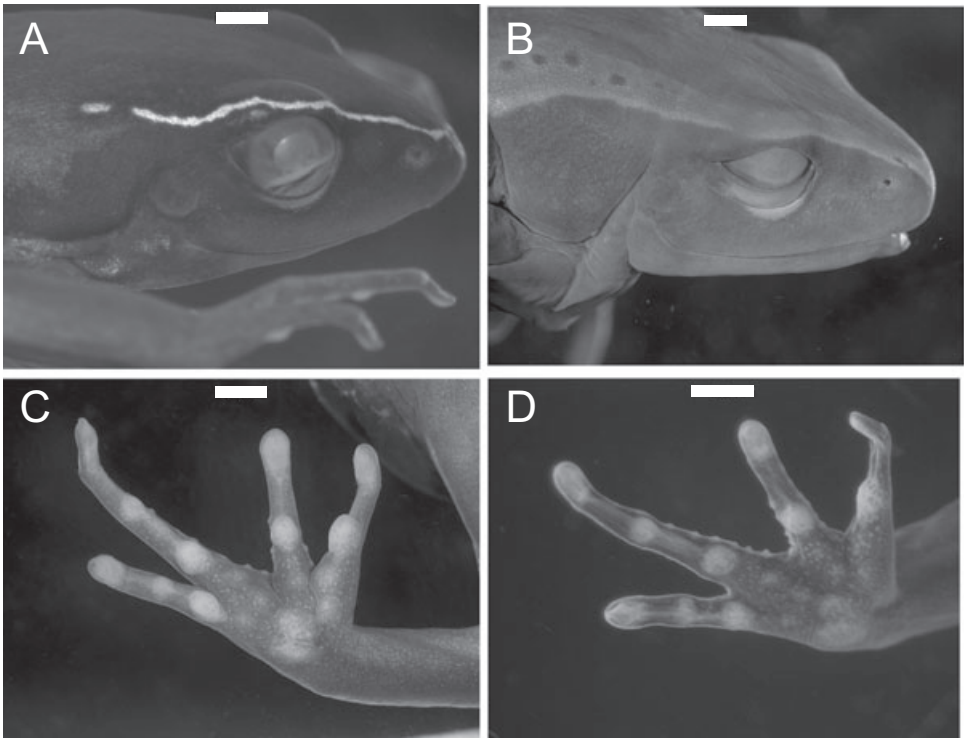

Figure 3. Right lateral view of the head of the holotypes of ***Cardioglossa manengouba* sp. nov.** (A; male; MCZ A-137909) and *C. oreas* (B; female; MHNG 1253.87). Note the small tympanum and the swelling and fold immediately above and behind the tympanum. Ventral view of the right hand of a male paratype of *C. manengouba* (C; MCZ A-136933) and male *C. oreas* (D; MCZ A-137922). Scale bar = 1 mm.

metacarpal tubercles poorly developed or lacking at proximal base of digits (Fig. 3B); manual digit tips barely swollen; no webbing between manual digits; pronounced small, white and terminally blunt spines on manual digits; unpaired and unpigmented subarticular tubercles rounded, globular projections surrounded by pigmented skin; tibiofibula just longer than femur; relative length of toes: IV > III > V > II > I; pedal digit tips slightly expanded laterally; no webbing between pedal digits; no inguinal spines.

Skin very smooth and not tuberculate; very faintly visible median skin raphe; gular skin only slightly distended relative to female; golden white supraorbital line extends posteriorly from rostrum and terminates just posterior to tympanum; ventral surface of manual and pedal digit tips unpigmented; dorsal surface of ultimate intraphalangeal joint unpigmented (more marked on manual digits I–III, less so on manual digit IV; also marked on pedal digits I–III, but only slight unpigmented transverse line on pedal digits IV–V).

Comments on adult skeletal morphology will be provided in a future publication on skeletal morphology in *Cardioglossa* and related genera.

Coloration: The colour in life varies from ruddy brown to brownish red (Fig. 2B). In alcohol, this coloration changes to chocolate brown with no remnants of the red coloration typical of living specimens. The lines that extend posteriorly from the snout are typically golden white in life, but are predominantly white in preserved specimens. The lines originate on the ventral surface of the rostral tip but do not contact the margin of the upper lip (Fig. 3A). In the holotype, the lines form two anastomoses just rostral to the nares and continue unbroken posteriorly until just behind the tympanum where there is a small break in the line before it terminates (Fig. 3A). In specimens other than the holotype, the supraorbital line is continuous along its entire length and has either no anastomoses (MCZ A-136933) or one and an incipient second (MCZ A-136908 and -910). In all specimens, the supratympanal line obviously terminates anterior to the axilla. The ventral and lateral surfaces of the body of preserved specimens, as well as all surfaces of the limbs, exhibit a fine golden flecking that is observable under a dissecting microscope. In both living and preserved specimens, the dorsal head pigmentation is a shade darker than the remaining dorsum. This slightly darker pigmentation

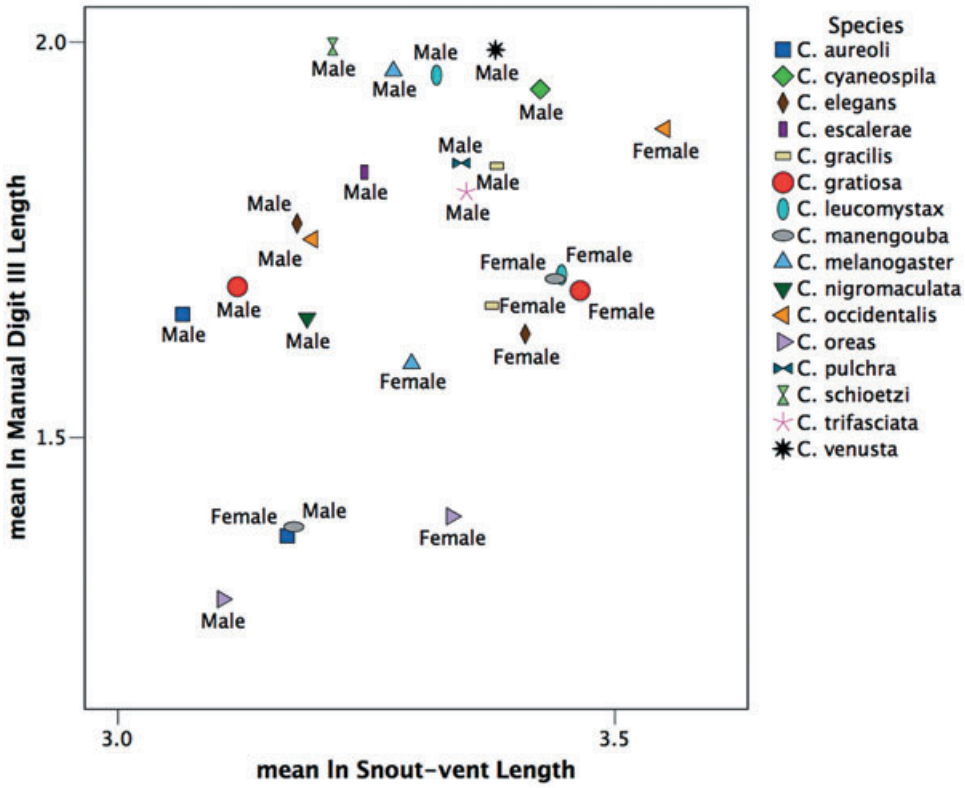

Figure 4. Scatter plot depicting mean length of third manual digit vs. mean snout–vent length for male and female of *Cardioglossa* species; data are ln-transformed. Males of both ***Cardioglossa manengouba* sp. nov.** and *C. oreas* are the only species examined in which no mature males have third manual digits absolutely longer than those of adult females of the same species. The mean value for males of *C. occidentalis* is somewhat low due to the inclusion of a specimen that may not be fully mature as it exhibits only weakly developed manual digital spines and a relatively short third manual digit.

extends posteriorly onto the lateral surface. The pigmentation surrounding the vent and in the inguinal region is similarly a darker shade, and in the latter case is mostly concentrated ventrally. The most posterior surface of the femur tends to exhibit lighter coloration and to be slightly golden. The holotype lacks accessory markings on the elbow or knee.

Measurements: Meristic data are provided in Table 1.

Variation: The single female *C. manengouba* is larger than the male specimens (*t*-test: $P = 0.048$; Table 1). Unlike all other *Cardioglossa* species except *C. oreas*, the third manual digit of male *C. manengouba* is not relatively longer than that of females (Fig. 4); there is no significant difference in the ratio of third manual digit length to snout–vent length between male and female *C. manengouba* (*t*-test: $P = 0.429$). While the third manual digit is not hypertrophied, male *C. manengouba* do exhibit well-developed spines on the medial surface of the third digit and lateral surface of the second digit (Fig. 3B; Table 1); on both digits, these spines are distributed in a single line extending proximodistally. In addition, males exhibit one or two weakly developed spines on the medial surface of the base of the second manual digit. The inner metatarsal tubercle of the female specimen (MCZ A-136910) is well developed and projects away from the pedal surface as a pronounced flange, most of the distal edge of which is unpigmented. In males, the inner metatarsal tubercle is much less developed and does not form a distinct and projecting flange. The lateral margins of the gular surface are slightly wrinkled in male specimens due to the slight distension of the gular skin in males. In addition to the two small palmar tubercles visible in the holotype, a third somewhat incipient tubercle is present proximal to manual digit I on the hands of MCZ A-136909, A-136910 and A-136933.

Distribution: Cardioglossa manengouba is known only from a small patch of gallery forest near the summit of Mt Manengouba (Fig. 1). If this species is indeed restricted to forests between 2100 and 2200 m

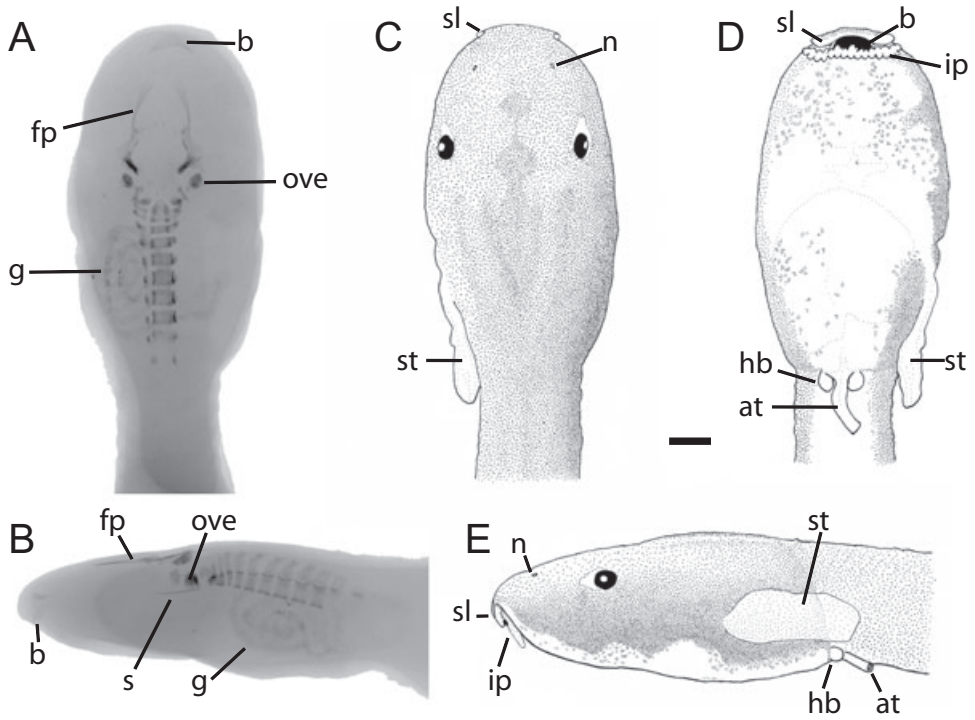

Figure 5. Tadpole of ***Cardioglossa manengouba* sp. nov.** (MCZ A-138156; Gosner stage 29/30). Radiographs of tadpole in dorsal (A) and lateral (B) views. Line drawings of tadpoles in dorsal (C), ventral (D) and left lateral (E) views. Scale bar = 1 mm. Abbreviations: at – anal tube; b – beak; fp – frontoparietal bone; g – gut; hb – hindlimb bud; ip – infraoral papillae; n – naris; ove – otic vesicle endolymph; s – sphenethmoid bone; sl – supraoral labium; st – spiracular tube.

elevation, it is unlikely to be found on other nearby mountains, such as Mt Kupe (summit elevation 2064 m) and Mt Nlonako (summit elevation 1825 m).

Natural history: All specimens were collected near shallow, sandy streams in montane gallery forest during the day (12:00–15:00 h) when they were active on the ground (Fig. 2A). The male holotype (MCZ A-137909) and female paratype (MCZ A-137910) were found in axillary amplexus hopping along a dry streambed with steep rock sides covered in damp, low-lying vegetation. Other specimens were found under rocks at the edge of a stream or hopping in leaf litter.

Conservation status: The entire range of this species is probably restricted to a very small patch of forest. As the two known localities are less than 3 km apart, the extent of occurrence is possibly less than 10 km^2. This species should be recognized as Critically Endangered following the IUCN (2001) criteria because *C. manengouba* is known only from forests near the summit of Mt Manengouba, has both a very restricted extent of occurrence and area of occupancy, and the extent and quality of the forest habitats in which it occurs are declining (Gartshore, 1986; Stuart, 1986b; Gonwouo *et al*., 2006; IUCN *et al*., 2006). The grasslands near the summit of Mt Manengouba are actively grazed by cattle, goats and horses owned by local Fulbe-speaking peoples. Some trails used by livestock pass through forest in which *C. manengouba* is found. Indeed, at the type locality a large muddy trail cuts across the stream and many cattle were crossing at the time specimens were collected.

Tadpoles: DNA sequence divergence between an adult *Cardioglossa manengouba* (MCZ A-136933) and a tadpole (MCZ A-138157) collected at the type locality is only 0.34%, and each of the eight nucleotide differences is the result of a gap in polynucleotide regions. This percentage difference is well within the range seen in intrapopulation comparisions in 16S rRNA sequence data in other frogs (Vences *et al*., 2005). Because of the high degree of similarity in this mtDNA sequence data, I assign this and other morphologically similar tadpoles collected syntopically with the adult type specimens to *C. manengouba*. The Gosner stages of the tadpoles examined (MCZ A-138153-59) range from stages 26 to 29 (i.e. all tadpoles examined exhibit very small hindlimb buds). Tadpoles were collected by dip-netting in the leaf litter and sandy soil of small shallow streams in gallery forest.

Table 1. Descriptive morphometrics of ***Cardioglossa manengouba* sp. nov.** All measurements are given in millimeters

Character	MCZ A-137909 Holotype Male	MCZ A-136933 Paratype Male	MCZ A-137908 Paratype Male	MCZ A-137910 Paratype Female
Snout–vent length	23.0	23.3	25.6	31.2
Head width	7.7	7.9	8.8	9.7
Tympanum height	1.0	1.3	1.4	1.5
Eye diameter	3.1	3.6	3.1	3.6
Snout length	2.2	2.2	2.7	2.9
Radioulna length	6.2	6.0	6.4	7.5
Manual digit I	2.0	2.3	2.3	2.9
Manual digit II	2.1	2.3	2.3	3.3
Manual digit III	3.8	4.1	4.1	5.5
Manual digit IV	2.5	2.8	2.7	3.2
Femur length	11.0	10.4	11.2	14.1
Tibiofibula length	11.6	11.6	11.7	15.3
Pedal digit I	1.8	1.9	1.6	2.0
Pedal digit II	2.8	2.8	2.6	3.3
Pedal digit III	4.5	4.5	4.2	5.3
Pedal digit IV	6.8	6.9	6.9	8.2
Pedal digit V	3.8	3.9	3.4	4.0
Inner metatarsal length	1.0	1.1	1.1	1.2
No. of spines on medial MDII	R – 2 L – 1	R – 2 L – 2	R – 2 L – 2	–
No. of spines on lateral MDII	R – 2 L – 4	R – 2 L – 2	R – 4 L – 3	–
No. of spines on medial MDIII	R – 3 L –	R – 5 L – 9	R – 10 L – 11	–

MDII, manual digit II; MDIII, manual digit III; R, right; L, left.

The eyes of the tadpole are small, the oral labia lack keratinous denticles, a large beak is present and the spiracle is a long, unpigmented funnel (Fig. 5). The body is ovoid and elongate as well as dorsoventrally compressed. In dorsal view, the small eyes are directed laterally and located well towards the midline such that they are not visible in ventral view (Fig. 5D). The external naris is extremely small, unornamented, possibly imperforate, and the margins are flush with the skin of the body. In preservative, the coloration of tadpoles of *C. manengouba* is a light greyish brown that is essentially solid with no spots or prominent markings. The ventral surface is transparent with only a few scattered melanocytes (Fig. 5D).

The supraoral labium is directed ventrally and the mouth is positioned such that neither papillae nor oral labia are apparent in dorsal view (Fig. 5C). The broad supraoral labium extends anteriorly and laterally from the rostrum, forming a pronounced angle between the anterior rostrum and the laterally projecting posterior surface of the labium (Fig. 5C); this labium is markedly hook-shaped in lateral view (Fig. 5E). In addition, the supraoral labium is mostly pigmented and smooth; the ventral margin is concave and accommodates the anterior margin of the keratinous upper beak. The infraoral labium exhibits two forms of projections: just posterior to the mouth, the surface of the infraoral labium is covered by many small subconical projections, whereas the lateral and posterior labial margins are covered in larger and slightly elongate lobular projections. The broad and wide keratinous upper beak exhibits a series of elongate, and slightly recurved, comb-like processes.

The spiracle is located on the posterolateral surface of the body (Fig. 5E). The spiracular tube is elongate, unpigmented and extends caudally nearly to the same anteroposterior level as the terminus of the anal tube; the distal opening is directed slightly ventrally. In preserved *C. manengouba* tadpoles, the spiracular tube extends caudally and the distal opening of the spiracular tube is directed ventrally. In many specimens, however, the distalmost spiracular tube is curved or bent, probably due to dehydration during the process of preservation.

The anal tube is unpigmented, the distal extent is free from the tail and in several specimens it tends to point sinistrally. Every tadpole exhibits a large yellow-white entity, probably the liver, that occupies most of the body cavity and either totally or mostly obscures the coiled gut. Using digital radiography, debris was clearly observed in the gut of four of the

seven tadpoles (Fig. 5B); it is thus inferred that these specimens were feeding prior to collection. There is no relationship between the presence of food in the gut and either body size or Gosner stage. The branchial basket, as viewed through the ventral body wall, is greatly elongate and extends well posterior to the heart.

The tail is very long and muscular. The large spinalis muscles extend onto the posterior dorsolateral surfaces of the cranium such that they form a 'Y' in dorsal view (Fig. 5C). The length of the body (as measured from the snout to the proximal base of the anal tube) constitutes only one-third or less of the total length of the tadpole. A tail fin is present along the entire ventral margin of the tail but is present only on the posteriormost two-thirds of the dorsal tail surface.

Digital radiography revealed that all tadpole specimens have dense calcified deposits in the cranial endolymphatic sacs and that all but two (MCZ A-138153-54) have similar deposits in the otic capsules (Fig. 5A, B). Two of the three largest tadpoles (MCZ A-138155 and 56; Gosner stages 26/27 and 29/30, respectively) exhibit significant ossification of the frontoparietal, parasphenoid, exoccipital, vertebral centra and neural spines (Fig. 5A, B). The centra and neural arches of all nine vertebrae, including the sacral vertebra, are visible. In addition, one pair of neural arches is visible posterior to the sacral vertebra, which represents the first ossification of the urostyle; no hypochord ossifications are present (Fig. 5B).

The tadpole of *C. manengouba* is morphologically similar to that of *C. occidentalis* (Blackburn *et al*., in press), the only other *Cardioglossa* species for which the tadpole has been fully described (Lamotte, 1961). In *C. occidentalis* the ventral surface is densely pigmented (Lamotte, 1961: fig. 2) whereas in *C. manengouba* it is largely transparent (Fig. 5D). The broad and projecting morphology of the supraoral labium of *C. manengouba* tadpoles is apparently absent in *C. occidentalis* (Lamotte, 1961: fig. 3). The infraoral labial morphology is similar in both species, but *C. occidentalis* differs by having more small subconical projections just posterior to the mouth (see fig. 3 in Lamotte, 1961). The spiracular tube is much longer relative to the length of the body in *C. manengouba* than in *C. occidentalis*. However, a very elongate spiracular tube is probably also present in other *Cardiglossa* species for which the tadpoles remain undescribed (e.g. Perret, 1966; Amiet, 1972b; Altig & McDiarmid, 2000).

Etymology: The specific epithet is a noun in opposition and refers to the type locality, Mt Manengouba.

Morphometric diversity

One-way ANOVA demonstrates that there are significant differences between species for all variables included in this analysis ($P < 0.01$). The first three principal component axes account for 87.7% of the total variance in these data (Figs 6, 7; Table 2). Plots of these three axes reveal three groups of similar species: (1) *C. gracilis*, *C. melanogaster* and *C. schioetzi*; (2) *C. escalerae* and *C. gratiosa*; and (3) *C. manengouba* and *C. oreas*. In addition, PCA reveals that *C. aureoli* occupies a region of morphospace distinct from other *Cardioglossa*. One-way ANOVA also shows that significant differences exist between species for each of the first three principal component axes ($P < 0.001$). Mean component scores of particular species (i.e. *C. aureoli*) or groups of species were compared with the mean for all other species using one-way ANOVA, and these comparisons reveal that the patterns observed through visual inspection of the plots are highly significant. Lastly, a conservative *post-hoc* test using a Bonferroni correction supports the species groups found through visual inspection of the PC plots (data not shown).

All 13 variables load strongly and positively on the first principal components axis (PC1), which accounts for 70.7% of the cumulative variance. This axis is here taken as a descriptor of body size. *Cardioglossa aureoli* exhibits strongly negative PC1 scores ($F = 23.388$, $P < 0.001$; Fig. 6); unsurprisingly, it is the smallest species of *Cardioglossa*. *Cardioglossa gracilis*, *C. melanogaster* and *C. schioetzi* all exhibit strong positive PC2 scores ($F = 210.674$, $P < 0.001$; Figs 6, 7); this axis accounts for 12.4% of the total variance and loads most positively on snout length and most negatively on eye diameter and inner metatarsal tubercle length (Table 2). In contrast, *C. escalerae* and *C. gratiosa* exhibit PC2 scores that are significantly more negative than other *Cardioglossa* ($F = 15.548$, $P < 0.001$; Figs 6, 7). Lastly, on the third axis, which loads strongly and positively on tympanum height and accounts for 4.6% of the cumulative variance, *C. manengouba* and *C. oreas* are differentiated from other *Cardioglossa* taxa by having the most negative scores ($F = 37.551$, $P < 0.001$; Fig. 7).

DFA of the morphometric data supports the results of the above PCA. Two different analyses were performed. In the first analysis, specimens were classified by species, whereas in the second analysis, specimens were assigned to classification groups. Specimens were assigned to classification groups by taking a mixed approach. First, the four groups found in the PCA were defined as classification groups: (1) *C. aureoli*; (2) *C. escalerae* and *C. gratiosa*; (3) *C. gracilis*, *C. melanogaster* and *C. schioetzi*; and (4) *C. manengouba* and *C. oreas*. Then, an additional

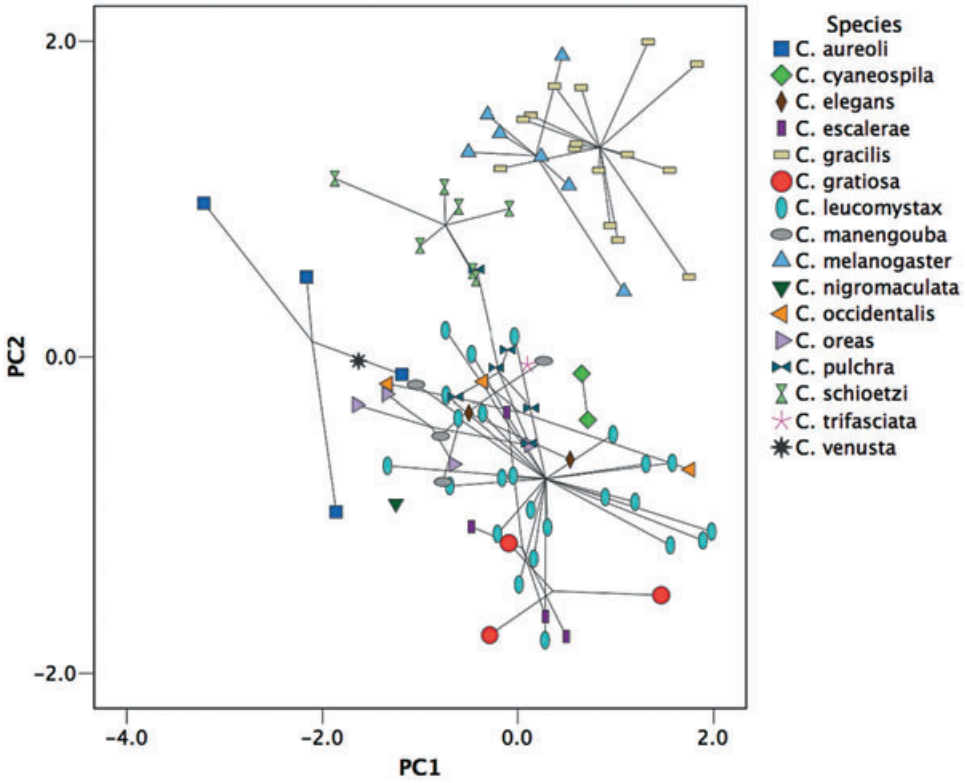

Figure 6. Scatter plot of the first and second principal component scores. The second principal component (PC2) is plotted against the first principal component (PC1), an indicator of body size. Lines are drawn to indicate the centroid of points for each species.

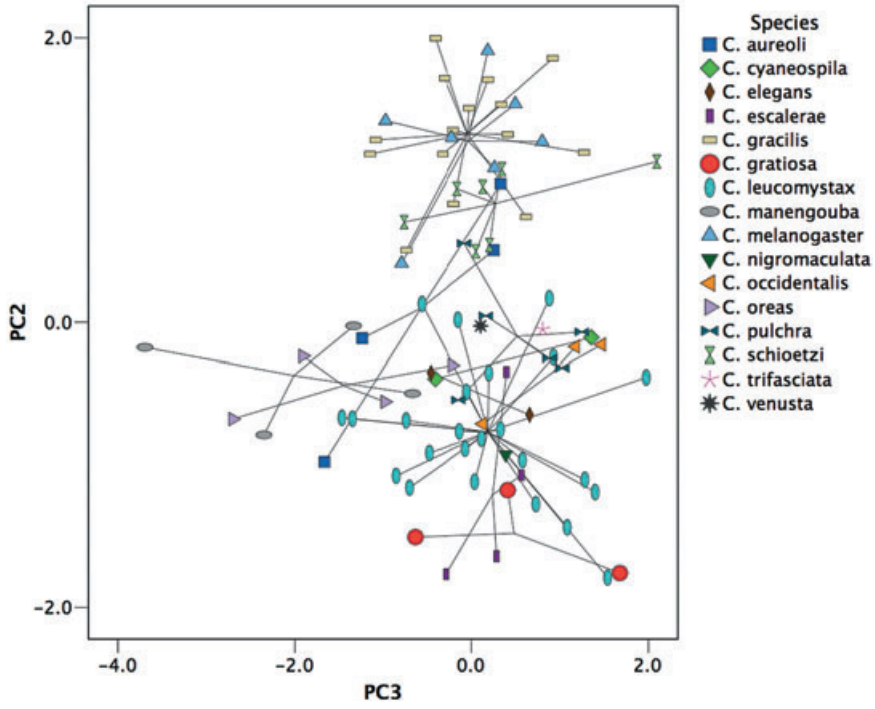

Figure 7. Scatter plot of the second and third principal component scores. The second principal component (PC2) is plotted against the third principal component (PC3). Lines are drawn to indicate the centroid of points for each species.

Table 2. Results of principal components analysis of morphometric data. Percentage variance, cumulative variance and loadings of morphometric variables for the first three principal component axes

	Eigenvalue	Percentage variance	Cumulative variance	Loadings of morphometric variables										
				SVL	HW	TH	ED	SL	FL	TFL	PDI	PDII	PDIII	PDIV	PDV	IMT
PCI	0.299	70.71	70.71	0.858	0.841	0.749	0.552	0.735	0.923	0.891	0.903	0.891	0.912	0.913	0.869	0.825
PCII	0.053	12.40	83.11	–0.161	–0.135	–0.163	–0.499	0.518	0.171	0.238	–0.009	0.113	0.217	0.233	0.373	–0.520
PCIII	0.019	4.56	87.67	0.129	0.060	0.557	0.141	0.200	0.015	0.033	–0.233	–0.228	–0.129	–0.069	–0.137	–0.065

SVL, snout–vent length; HW, head width; TH, tympanum height; ED, eye diameter; SL, snout length; FL, femur length; TFL, tibiofibula length; PDI–V, pedal digit I–V length; IMT, inner metatarsal tubercle length.

Table 3. Values of Wilks' λ and χ^2 resulting from discriminant function analysis are presented for the defined functions

Functions	Wilks' λ	χ^2	d.f.	*P*
1–4	0.007	246.12	28	<0.001
2–4	0.057	140.56	18	<0.001
3–4	0.259	66.14	10	<0.001
4	0.664	20.04	4	<0.001

classification group was created based on Amiet (1972a, 1975, 1981): (5) *C. pulchra*, *C. venusta* and *C. trifasciata*. Five species were not assigned to any group: *C. cyaneospila*, *C. elegans*, *C. leucomystax*, *C. nigromaculata* and *C. occidentalis*. Two of these species, *C. elegans* and *C. leucomystax*, have previously been included in a larger group containing group 3 of the present analysis, but neither species was recognized as having a sister-species relationship to another species (Amiet, 1981). In addition, Amiet (1981, 1987) considered *C. nigromaculata* to be the sister species of *C. gratiosa*, and thus *C. nigromaculata* is predicted to be assigned to group 2 using DFA. The other two unassigned species, *C. cyaneospila* and *C. occidentalis*, have not been included in previous studies of *Cardioglossa* relationships; the latter species was only recently described (Blackburn *et al*., in press). The ability of DFA to assign specimens correctly was tested for the five classification groups.

The first analysis tested the ability of the morphometric data to discriminate between species. This DFA was performed specifically to determine whether specimens classified a priori as a particular species were more likely to be misclassified as another species in the same classification group used in the second analysis. Eleven functions were defined, although only the first five were significant (χ^2: $P < 0.005$), and 11 of the 13 morphometric characters entered into the stepwise discrimination function before discriminating power was exhausted. The characters not included were head width and the length of pedal digit II. Only eight of the 88 specimens were misclassified. In the second analysis, five of these eight specimens are assigned to a classification group and, in this first analysis, all were misclassified as another species in the same classification group. These misclassifications support the species groups used in the second analysis.

In the second analysis, four functions, all with low Wilks' λ-values, were defined (χ^2: $P < 0.001$), and seven of the 13 characters entered into the stepwise discrimination function before discriminating power was exhausted (Table 3). The six characters not included in the DFA are head width, femur length,

tibiofibula length, and the lengths of pedal digits II, III and V. The 56 specimens assigned a priori to a specific classification group were classified correctly in 98.2% of cases; only one specimen (*C. escalerae*, TNHC 38698) was misclassified. Both specimens of *C. cyaneospila* were classified as belonging to group 5 with *C. pulchra*, *C. venusta* and *C. trifasciata*. The number of *C. leucomystax* specimens assigned to each of the classification groups is as follows: (1) two specimens; (2) 11 specimens; (3) no specimens; (4) three specimens; (5) eight specimens. In five cases, the likelihood that the *C. leucomystax* specimen is classified incorrectly is significant ($P(D > d \mid G = g) < 0.05$). One male specimen of *C. occidentalis* (FMNH 83121) was classified as group 5, the other male (FMNH 83122) as group 4, and the female specimen (MVZ 244911) was classified as belonging to group 2; however, the likelihood that FMNH 83121 and MVZ 244911 are misclassified is significant ($P(D > d \mid G = g) < 0.05$). The female specimen of *C. elegans* (BMNH 1947.2.30.35) was assigned to group (2) and the male specimen (UTA A44472) to group (4); in both cases, the likelihood that the specimen is misclassified is not significant.

DISCUSSION

Relationships of *Cardioglossa manengouba*

Both PCA and DFA reveal that *Cardioglossa manengouba* is morphologically similar to *C. oreas*, a high-altitude species restricted to Cameroon. These species share several morphological similarities to the exclusion of most other Cameroonian *Cardioglossa*. Both species exhibit small tympana, which are indistinct in *C. oreas*, a pronounced swelling in the skin immediately posterior to the tympanum that is often accompanied by a fold in the skin immediately above and behind the tympanum, and males of both species lack a hypertrophied third manual digit (Fig. 3). In addition, both species lack the small inguinal spines that are present in mature males of all other *Cardioglossa* except *C. escalerae* (my unpubl. data). Currently, the call of both species remains unknown (*C. oreas*: Amiet, 1973). Unique among *Cardioglossa*, these two species exhibit a general reduction or loss of typical male secondary sexual characters, which may reflect a close phylogenetic relationship. Amiet (1981) recognized *C. oreas* as distinctive among *Cardioglossa* because he observed that males lack both a hypertrophied third manual digit and spines on the manual digits. However, the two male *C. oreas* examined in this study (MCZ A-137922, A-137928) exhibit spines on the medial surface of the third digit and on both the lateral and the medial surfaces of the second digit (Fig. 3B). Similar to Amiet's (1981) observation of *C. oreas*, Herrmann *et al*. (2004) suggested that a lack of spines on the hypertrophied manual digits of male *C. alsco* is a unique characteristic. Yet given the new data on the presence of manual digital spines in male *C. oreas*, I urge caution in interpreting the presence or absence of this character. The spines can be difficult to see without the aid of a microscope or hand lens, and this character may exhibit seasonal polyphenism in other arthroleptid taxa (e.g. Schmidt & Inger, 1959). *Cardioglossa manengouba* and *C. oreas* constitute two of the three species with the highest elevational ranges in Cameroon (the third, *C. alsco* from Tchabal Mbabo, was not included in this study). Whereas *C. manengouba* is known only from Mt Manengouba, *C. oreas* is documented from the Bamboutos Mountains (Amiet, 1972a; present study), Mt Oku (Amiet, 1987; present study) and Mt Lefo (Böhme, 1975). In addition, Amiet (1987) states that *C. oreas* is present on Mt Manengouba, but no details of this record are provided; I did not find this species during fieldwork on Mt Manengouba in either 2004 or 2006. Based on morphological data, it seems likely that *C. manengouba* and *C. oreas* are sister taxa. If so, then vicariance between the forests of Mt Manengouba and other mountains to the north-east may have resulted in the allopatric speciation of these taxa. If *C. oreas* is present on Mt Manengouba, it may have later colonized this mountain at a time when the montane forests were continuous, or nearly so, between Mt Manengouba and the mountains to the north-east.

Tadpole morphology and ecology

The only previously described *Cardioglossa* tadpole is that of *C. occidentalis* (Lamotte, 1961; Blackburn *et al*., in press). Both Amiet (1972b) and Perret (1966) provide illustration of a *C. gracilis* tadpole but these are not accompanied by a description; however, as figured, the tadpole morphology generally agrees with that discussed here. The tadpole of *C. manengouba* is similar to *C. occidentalis* in lacking keratinous denticles on the labia and in having a large and pronounced beak, a large suboral flap with numerous digitform projections, and an elongate, unpigmented, funnel-shaped spiracle. However, this elongate spiracle appears to be relatively longer in *C. manengouba*. Lamotte (1961) noted that the strong ventral pigmentation of *C. occidentalis* separates it from other tadpoles including those of *Phrynobatrachus*. In contrast, *C. manengouba* exhibits almost no ventral pigmentation.

Tadpoles of *Cardioglossa* are typically collected in leaf litter or deposits of sediment in shallow streams (Amiet, 1972b; Rödel, Schorr & Ernst, 2001; my unpubl. data; present study). Interestingly, the morphology of *C. manengouba* tadpoles bears a striking resemblance to that of the South American microhylid

Table 4. Proposal for *Cardioglossa* species groups based on results of this study

Species	Altitudinal range (m)	Source	Altitudinal zone	Country range
C. aureoli	< 700	S	Lowland	Sierra Leone
C. escalerae	< 1100	A72, L72	Lowland	Cameroon, CAR, DRC, Equatorial Guinea
C. gratiosa	< 1200	A72, Bö	Lowland	Cameroon, Equatorial Guinea, Gabon, Nigeria
C. nigromaculata	< 800	A72	Lowland	Cameroon, Equatorial Guinea, Gabon, Nigeria
C. gracilis	< 1200	I	Lowland	Cameroon, CAR, DRC, Equatorial Guinea, Gabon
C. melanogaster	1200–1700	A72, U	Montane	Cameroon, Nigeria
C. schioetzi	1640–1950	A81, B06	Montane	Cameroon, Nigeria
C. alsco	2100	H04	Montane	Cameroon
C. cyaneospila	1800–1850	L50	Montane	Burundi, DRC, Rwanda
C. pulchra	1200–2050	A72, U	Montane	Cameroon, Nigeria
C. venusta	950–1250	A72, H05	Submontane	Cameroon
C. trifasciata	1750–1800	A72	Montane	Cameroon
C. manengouba	2160–2190	*	Montane	Cameroon
C. oreas	1900–2650	A72, U	Montane	Cameroon
Species of uncertain affinity				
C. elegans	< 500	I	Lowland	Cameroon, Equatorial Guinea, Gabon
C. leucomystax	< 1200	A72, B, I	Lowland	Cameroon, CAR, DRC, Equatorial Guinea, Gabon, Nigeria, RC
C. occidentalis	< 650	B, R	Lowland	Ghana, Guinea, Ivory Coast, Liberia, Sierra Leone

Country abbreviations: CAR, Central African Republic; DRC, Democratic Republic of Congo (Kinshasa); RC, Republic of Congo (Brazzaville). Sources for altitudinal ranges (in metres above sea level): A72, Amiet (1972a); A81, Amiet (1981); B06, Blackburn (2006); B, Blackburn *et al*. (in press); Bö, Böhme & Schneider (1987); H04, Herrmann *et al*. (2004); H05, Herrmann *et al*. (2005b); I, IUCN *et al*. (2006); L50, Laurent (1950); L72, Laurent (1972); R, Rödel *et al*. (2001); S, estimated based on Schiøtz (1964); U, D. C. Blackburn, unpubl. data; *present study.

Otophryne robusta, which has unusual, fossorial tadpoles (Wassersug & Pyburn, 1987). *Cardioglossa manengouba* tadpoles were collected syntopically with tadpoles of *Astylosternus*, *Leptodactylodon* and *Leptopelis*, all of which were collected by dragging a dip-net through leaf litter and sandy soil. However, only *Cardioglossa* tadpoles exhibit strong similarities to that of *Otophryne*. These similarities include a dorsoventrally flattened body, small eyes, a ventrally positioned mouth, a long tail and a greatly elongated spiracle. *Cardioglossa* is the only anuran genus with a spiracular tube that approaches the length found in *Otophryne*, although it is unclear whether it would function similarly to that of *Otophryne*. As the length of the spiracular tube relative to body length changes during *O. robusta* ontogeny (Wassersug & Pyburn, 1987), it is possible that the spiracular tube of *C. manengouba* could be even longer relative to body length at other points in its ontogeny. The elongate branchial basket of *C. manengouba* is unusual and may also be related to a fossorial ecology, but its functional implications are unclear. Further examination of *Cardioglossa* tadpole morphology, including chondrocranial anatomy, will elucidate the amount of covergence between *Cardioglossa*, *Otophryne* and other anuran species with fossorial tadpoles.

Implications of morphometric analyses for *Cardioglossa* systematics

The analysis of morphometric data presented here supports a close phylogenetic relationship between *C. manengouba* and *C. oreas*. In addition, this study allows for the recognition of other *Cardioglossa* species groups, which are discussed below (Table 4).

This study demonstrates that *C. aureoli*, from the Freetown Peninsula of Sierra Leone, is morphologically distinct from other *Cardioglossa* species. Based presumably only on coloration, this species was originally placed in *Cardioglossa* by Schiøtz (1964). Unlike other *Cardioglossa*, this species is typically found far from water (Schiøtz, 1964), thus possibly exhibiting some form of development in which there is no free-living and/or feeding tadpole (e.g. IUCN *et al*., 2006). DNA sequence data from the mitochondrial 16S ribosomal RNA gene indicates that this species is very

divergent (> 15%) from other *Cardioglossa* (Blackburn *et al*., in press), and molecular phylogenetic analysis shows that *C. aureoli* probably is more closely related to other arthroleptid species than to *Cardioglossa* (my unpubl. data). *Cardioglossa aureoli* is well separated from other *Cardioglossa* along PC1 (Fig. 6), which is largely an indication that both males and females of this species are much smaller than other *Cardioglossa* species. Molecular phylogenetic research and study of skeletal anatomy will probably reveal that *C. aureoli* should either be included in another arthroleptid genus or placed in its own genus.

Amiet (1987) suggested a close relationship between *C. gratiosa* and *C. nigromaculata*, both lowland species, and intimated the existence of a hybrid zone between these species in southern coastal Cameroon. This conclusion was based on the mixture of vocalization characteristics found in these populations (Amiet, 1987), but there is no reason why this mixture necessitates the hybridization of these species. There are no striking morphological or colour pattern similarities between *C. gratiosa* and *C. nigromaculata* and, although the sample sizes are extremely small, no obvious pattern emerged from PCA to support the similarity of these species to the exclusion of other species. In contrast, PCA reveals that *C. gratiosa* is morphologically similar to *C. escalerae*, another lowland species that is more widespread in Central Africa. Interestingly, in the DFA, *C. nigromaculata* was assigned to the classification group comprising *C. escalerae* and *C. gratiosa*. Amiet (1981) proposed a close phylogenetic relationship between these three species. The results of these morphometric analyses support this hypothesis and suggest that this species grouping should continue to be recognized.

Cardioglossa melanogaster and *C. schioetzi* are similar morphologically, ecologically and acoustically, and both are distributed throughout the mountains of Cameroon and Nigeria (Amiet, 1972a, 1981; Blackburn, 2006; Blackburn *et al*. in press). Amiet (1981) commented extensively on the similarities between *C. melanogaster* and *C. schioetzi* and hypothesized that these species may be closely related to *C. leucomystax* and *C. gracilis* (Amiet, 1975, 1981). The calls of *C. melanogaster* and *C. schioetzi* are very similar and differentiated mostly by the former species having longer notes with greater spacing between the notes (Amiet, 1981). In addition, the first two presacral vertebrae of *C. melanogaster* and *C. schioetzi* are fused (Blackburn *et al*., in press), which is the same conditition found in *C. gracilis* but absent in nearly all *C. leucomystax* examined (exceptions: USNM 563696, 563697 and 563705, all from low altitudes on Mt Nlonako in Cameroon). The plots of principal component scores reveal that both *C. melanogaster* and *C. schioetzi* are morphologically similar to *C. gracilis* but are easily distinguished from *C. leucomystax* (Fig. 6). In all three of the former species the distance from the anterior margin of the eye to the tip of the rostrum is subequal to or greater than the anteroposterior diameter of the eye. The results of the DFA further emphasize the dissimilarity between *C. leucomystax* and the three other species because specimens of *C. leucomystax* were classified as belonging to every group except the one comprising *C. gracilis*, *C. melanogaster* and *C. schioetzi*. Based on the available evidence, I propose that *C. melanogaster* and *C. schioetzi* are sister taxa and more closely related to *C. gracilis* than to *C. leucomystax*.

The recently described *C. occidentalis* is very similar in both appearance and biology to *C. leucomystax* with which it was long recognized as conspecific (Blackburn *et al*., in press). If *C. occidentalis* and *C. leucomystax* are sister species, then they exhibit a biogeographical pattern similar to sister pairs of other vertebrates found in the Upper and Lower Guinean Forest Zones (Blackburn *et al*., in press). The results of the morphometric analyses presented here are equivocal with regard to the relationship of these two species; there is no strong evidence for either morphometric similarity or dissimilarity. In the DFA, no specimens of *C. occidentalis* or *C. leucomystax* were assigned to the classification group consisting of *C. gracilis*, *C. melanogaster* and *C. schioetzi*. Similarly, the three classification groups to which *C. occidentalis* specimens were assigned (groups 2, 4 and 5) are the same three groups to which nearly all *C. leucomystax* specimens were assigned. The PCA and DFA reveal a substantial amount of morphometric diversity within these two species, but the analyses also suggest that they exhibit a similar range of morphometric diversity. Phylogenetic analyses will be required to elucidate the relationship between these two species as well as their relationship to other *Cardioglossa*.

Based in part on both ecology and coloration, Amiet (1972a, 1975, 1981) argued that three montane taxa, *C. pulchra*, *C. trifasciata* and *C. venusta*, have close affinities to one another. All three species exhibit a bluish ventral coloration and dorsal skin that is covered in relatively larger tubercles than other *Cardioglossa* species. The scores for the first three PC axes for these three species were not significantly different from those of other species, but the species do occupy a similar region of morphospace (Fig. 6). Interestingly, DFA correctly classified all specimens assigned to this classification group. This lends further support to the similarities recognized by Amiet (1972a). All three species exhibit small ranges in the mountains of the Cameroon Volcanic Line and *C. trifasciata* is found only on the verdant south-west

slopes of Mt Manengouba. While I was unable to examine specimens of *C. alsco* for this study, I have followed Herrmann *et al*. (2004) by including this recently described species in this species group based on a blue ventral coloration, a granular dorsal skin, and a high similarity of both coloration and pattern to *C. pulchra*.

Most previous studies of *Cardioglossa* diversity have not included *C. cyaneospila*, a species endemic to the mountains of Rwanda and Burundi (e.g. Amiet, 1972a, 1981; Herrmann *et al*., 2004). The two specimens of *C. cyaneospila* included in this study were among the largest of all *Cardioglossa* males examined. Similar to *C. oreas*, *C. pulchra*, *C. trifasciata* and *C. venusta*, *C. cyaneospila* lacks an infratympanal line and exhibits small, scattered tubercles and like *C. elegans*, *C. nigromaculata* and *C. trifasciata*, the dorsal markings in *C. cyaneospila* are large and block-like. Based on the PCA, this species is clearly differentiated from *C. gracilis*, *C. melanogaster* and *C. schioetzi* but not other *Cardioglossa* species. *Cardioglossa cyaneospila*, *C. pulchra*, *C. trifasciata* and *C. venusta* do not form a group that can be easily differentiated from other *Cardioglossa* because of extreme values of the first three PC axes, but all three occupy a similar region of morphospace. In the DFA, both specimens of *C. cyaneospila* were assigned to the group consisting of *C. pulchra*, *C. trifasciata* and *C. venusta*. In light of the other similarities mentioned above, it seems reasonable to consider *C. cyaneospila* to be part of this species group. As all of these species are montane, this species group can be taken as further support for the historical continuity of montane faunas of different regions in Africa.

Because *C. cyaneospila* is known only from type specimens and the type locality is located in a conflict zone [Bururi Province, Burundi; erroneously listed by Frost (2006) as the Democratic Republic of Congo], it is unlikely that specimens for molecular phylogenetic research will be available in the near future. Another taxon from a nearby conflict zone, *C. nigromaculata inornata* from Fizi in the South Kivu Province in eastern Democratic Republic of Congo, probably represents a distinct species (Frost, 2006) but specimens were unavailable for study. Our poor understanding of the relationships and taxonomy of these two Central African montane taxa emphasizes the necessary place of morphometric and morphological analyses in studies of diversity in *Cardioglossa* and other Central African taxa that occur in conflict zones (for a similar example, see Ohler, 1996).

Diversity and distribution of *Cardioglossa*

Geographical patterns of diversity within *Cardioglossa* are of particular interest to studies of African biogeography for two principal reasons. First, it is an excellent group within which to study relationships within and between ecoregions (e.g. forests of Cameroonian and Albertine Rift mountains) as well as between large regions such as western and central Africa. Second, because *Cardioglossa* consists of approximately equal numbers of montane and lowland species, it is an interesting opportunity to understand the connections between montane biota of different regions, the connections of montane faunae within the Cameroonian mountains, and the interspecific relationships of a lineage with many montane and lowland species.

Studies of avian diversity in the many mountains of the Cameroon Volcanic Line have focused on phylogeography and the degree of faunal similarity among different Cameroonian mountains (Smith *et al*., 2000; Graham *et al*., 2005). Graham *et al*. (2005) found that the five mountains with the highest number of endemic avian species are Mt Cameroon ($N = 16$), Mt Manengouba ($N = 16$), Bakossi ($N = 15$), Obudu Plateau ($N = 15$) and Mt Kupe ($N = 14$). Within the Cameroonian mountains, Mt Manengouba has the highest chameleon diversity, which includes two taxa (*Chameleo perreti* and *Chameleo quadricornis quadricornis*) that are known only from Mt Manengouba and neary mountains (Gonwouo *et al*., 2006). Similar to these patterns of species diversity, the geographical distribution of *Cardioglossa* diversity exhibits a high concentration on Mount Manengouba. Four anuran species are strictly endemic to Mount Manengouba (*C. manengouba*, *C. trifasciata*, *Leptodactylodon erythrogaster*, and *Phrynobatrachus manengoubaensis*) and a number of other species are found only on Mount Manengouba and/or several other nearby mountains (e.g. *Astylosternus perreti*, *C. venusta*, *L. mertensi*, *L. ornatus ornatus*, *Petropedetes perreti*, *Werneria submontana*, *W. tandyi* and *Xenopus amieti*). This diverse anuran fauna further emphasizes that Mt Manengouba and the nearby mountains, including Nlonako, Kupe and Bakossi, are important centres of Cameroonian vertebrate diversity (Stuart, 1986a; Graham *et al*., 2005; Herrmann *et al*., 2005a, b).

Graham *et al*. (2005) also conducted cluster analyses of faunal similarity of montane species and montane endemic species and subspecies. Each of these analyses indicates that the faunae of the mountains of Manengouba, Kupe, Nlonako and Bakossi are more similar to each other than to the faunas of the mountains associated with the Bamiléké Plateau to the north, which include Bamboutos, Mbam and Oku. Examination of the three *Cardioglossa* species groups containing montane species shows that these species do not follow the patterns found by Graham *et al*.

(2005). For example, *C. oreas* is documented from Manengouba as well as Bamboutos and Oku, *C. venusta* is known from Manengouba and the southern part of the Bamiléké Plateau, and *C. melanogaster* is known from both Manengouba and Bamboutos. In addition, the number of endemic species found on Mt Cameroon is very different between birds and frogs. Mount Cameroon harbours as many endemic avian species as Mt Manengouba, but it has little endemic amphibian diversity. Only two species, *Leptodactylodon bueanus* and possibly *Werneria preussi*, are strictly endemic to the slopes of Mt Cameroon and both occur at low elevations below 1200 m. These differences between avian and anuran diversity indicate that history and local environment have differently affected the diversification of vertebrate lineages within the mountains of the Cameroon Volcanic Line.

Studies of geographical patterns of biodiversity are also important for developing an understanding of the relationship between faunas of different regions. One might predict that species at the edge of the geographical range of a genus would be most similar to neighbouring species. Thus species in one geographical region would be more similar to one another than to species from another region. In *Cardioglossa*, this is most applicable to two species, one found at the extreme western edge, *C. aureoli* in Sierra Leone, and the other at the extreme eastern edge of the range of the genus, *C. cyaneospila* in the Albertine Rift mountains. The nearest species to these species are *C. occidentalis* in the Upper Guinean Forest Zone and *C. escalerae* and *C. leucomystax* in the Congo River basin (Laurent, 1972). The present morphometric study shows that *C. aureoli* is distinct from all other *Cardioglossa*, including the nearby *C. occidentalis*, and that *C. cyaneospila* is morphologically similar to three species that are found only in the mountains of Cameroon. This hints at an underlying pattern of phylogenetic relationships that is more complex than a phylogeny in which species in similar geographical regions are more closely related to one another. Two of the species groups supported by this analysis are strictly montane, whereas another comprises strictly lowland forms (Table 4). Somewhat surprisingly, only one group contains both a lowland species (*C. gracilis*) and montane species (*C. melanogaster* and *C. schioetzi*), and the remaining species of uncertain affinities are all lowland. Future work should focus on resolving the phylogenetic relationships of these species groups, which are defined based on morphological data. Is morphological similarity indicative of close phylogenetic relationship or is there something about the ecology of montane or lowland species that is driving morphological similarity in different lineages? Did *Cardioglossa* originate in the mountains and then colonize the lowlands or, conversely, have there been multiple invasions of the mountains? Answering these questions about the relationships within and between *Cardioglossa* species groups using phylogenetic methods promises to shed light on the evolutionary history underlying the geographical and altitudinal distribution of sub-Saharan vertebrates.

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APPENDIX 1

KEY TO THE SPECIES OF *CARDIOGLOSSA*

1a. White or grey infratympanal line 2
1b. Infratympanal line absent 3
2a. Dorsal base coloration somber apple or olive green in life with blue near the base of the thigh (Amiet, 1972b; Laurent, 1972); infratympanal line weakly developed (possibly absent) and does not extend rostral to the tympanum (for photograph in life, see Amiet, 1972b) ..... *Cardioglossa escalerae*
2b. Infratympanal line strongly developed 4
3a. Three prominent and distinct dorsal markings present: subtriangular cephalic lobe, and subrectangular scapular and lumbar lobes 5
3b. No prominent and distinct dorsal markings (i.e. cephalic, scapular, and lumbar) 6
4a. Infratympanal line extends rostral to tympanum 7
4b. Infratympanal line does not extend rostral to tympanum and typically terminates immediately ventral to tympanum 8
5a. Skin of dorsal and lateral surfaces mostly smooth with some small scattered tubercles; in life, dorsal and lateral surfaces bluish lead grey with large blackish steel blue spots (Laurent, 1950); ventral surface of body and hindlimbs covered by anastomosing network of wide, dark grey bands interspersed with greyish cream coloration ..... *C. cyaneospila*
5b. Skin densely covered in large, closely spaced tubercles; in life, dorsum and limbs grey and ventral surface deep, dark blue (Amiet, 1972a); three prominent dorsal markings large and blockish (for photograph in life and variation in pattern and fusion, see Amiet, 1972a, b) ..... *C. trifasciata*
6a. Dorsal base coloration bright orange or yellow in life; many irregularly shaped and distributed black or dark brown spots, some of which may be symmetrical with respect to midline ..... *C. aureoli*
6b. Dorsal base coloration not bright orange or yellow in life (but possibly golden or tan) 9
7a. Infratympanal line merged with labial bar forming continuous, or nearly so, thick white bar that extends from rostrum to level of tympanum (for photograph in life, see Amiet, 1972b) ..... *C. gracilis*

7b. Infratympanal line typically very distinct and curves rostrodorsally towards external naris……10
8a. Dorsal base coloration orange or reddish in life with block-like black dorsal markings; scapular and lumbar markings typically fused into continuous black rectangle (for photograph in life and variation in dorsal pattern, see Amiet, 1972a, b, c, respectively)……*C. nigromaculata*
8b. Continuous black mask on lateral surface extends from rostrum to approximate snout–vent midpoint……11
9a. Three dorsal markings completely or mostly confluent; tan dorsal base coloration present as continuous band extending dorsolaterally from snout to inguinal region; bluish black ventral coloration……12
9b. Three dorsal markings absent or present only as scattered dots (occasionally present as a confluent band in *C. oreas*; see figure 8 of Amiet, 1972a)……13
10a. Large blocky dorsal markings approximately the same dark shade as lateral markings (for photograph in life, see Amiet, 1972b, c); dorsal markings typically ring-shaped with small central area of lighter coloration; brightness of infratympanal line less intensity anterior to tympanum; distance from anterior orbit to tip of rostrum less than anteroposterior length of eye; expanded digit tips……*C. elegans*
10b. In both life and preservation, dorsal markings distinctly lighter than lateral markings……14
11a. Dorsal base coloration reddish or orangish brown with markings on lateral surface ranging from red to yellow (Amiet, 1972a; for colour photograph, see Alonso *et al*., 2006); large, prominent and rounded inguinal spot; dorsal markings indistinct or poorly developed (for variation in lateral and dorsal markings, including photographs in life, see Amiet, 1972a, b)……*C. gratiosa*
11b. Prominent, thick white infratympanal line; dorsal markings well developed; inguinal spot small and somewhat irregularly shaped……*C. occidentalis*
12a. Three dorsal markings 'faded and conjoined to various degrees' (Herrmann *et al*., 2004), not forming distinct, solid, and wide band extending from rostrum to vent; dorsal markings appear as varied shades of dark tan or brown; inguinal spot similar to rostral mask as distinct from and much darker than dorsal markings (based on colour photograph of fig. 2a of Herrmann *et al*., 2004)……*C. alsco*
12b. Very distinct, solid, wide black or dark brown band extends from rostrum to vent (for black and white or colour photograph in life, see Amiet, 1972b or 1989, respectively); dark shade of inguinal spot similar to that of rostral mask and dorsal band; inguinal spot fused medially to dorsal band……*C. pulchra*
13a. No dorsal markings; dorsal base coloration is brownish red in life; prominent white line extends from rostral tip along canthus rostralis and terminates just posterior to level of tympanum; male lacks elongate manual digit III……*C. manengouba*
13b. Scattered small dorsal markings, intraspecifically irregular in both number and position……15
14a. Broad connection between cephalic and scapular dorsal markings (for photographs in life, see Amiet, 1972b); solid, or nearly so, black or dark brown stripe extends proximodistally on posterior femur; ventral surface of body (i.e. belly) mostly white or cream and covered in diffuse pigmentation and/or large spots; toe tips not expanded ……*C. leucomystax*
14b. Cephalic and scapular dorsal markings either not connected or connected by narrow band; ventral surface darkly pigmented, possibly with scattered white or silver flecks; first two presacral vertebrae always fused; toe tips expanded……16
15a. Indistinct tympanum; in life, ventral surface varies from black to dark brown and dorsum yellow or golden (grey in preserved specimens) with scattered, irregularly positioned dark brown or black markings (for variation of dorsal pattern, including photographs in life, see Amiet, 1972a, b); males lack elongate manual digit III ……*C. oreas*
15b. Prominent tympanum; dorsal base coloration rosy beige in life with black or brownish spots or mottling; ventral surface of body and hindlimbs greenish blue in life; prominent bars on both femur and tibiofibula; few scattered markings on dorsum (remnants of the three dorsal markings) sometimes form 'mirror-image' pairs with respect to midline (for photograph in life and variation in dorsal pattern, see Amiet, 1972a, b)……*C. venusta*
16a. Ventral surface nearly solid black or very dark brown; mask extends caudally from rostrum and is broken into many small spots posterior to tympanum (for variation of dorsal pattern and photograph in life, see Amiet, 1972a, b, 1975); distance from anterior orbit to tip of rostrum subequal to or slightly less than anteroposterior length of eye……*C. melanogaster*
16b. Ventral surface black or dark brown with many silver white flecks; solid mask extends posteriorly to approximately caudal extent of scapular lobe (similar to *C. occidentalis*), distance from anterior orbit to tip of rostrum greater than the anteroposterior length of eye……*C. schioetzi*

APPENDIX 2

SPECIMENS EXAMINED

C. aureoli – ZMK R075881 (male holotype, 22.4 mm), ZMK R075885 (male paratype, 20.5 mm), ZMK R075586 (female paratype, 23.6 mm), CAS 230187 (female, 24.1 mm), Sierra Leone, Freetown.

C. cyaneospila – KU 154326 (male, 31.0 mm), KU 154327 (male, 30.7 mm) Burundi, Bururi.

C. elegans – BMNH 1947.2.30.35 (female holotype, 30.2 mm), Cameroon, Efulen; UTA A44472 (male, 23.5 mm), Cameroon, Ntale Plateau, Southwest Province.
C. escalerae – TNHC 38697 (male, 24.6 mm), TNHC 38698 (male, 25.7 mm), Cameroon, Ototomo Forest Reserve, Center Province; TNHC 47888 (male, 25.4 mm), TNHC 47889 (male, 26.5 mm), Cameroon, Mt Kala, Center Province.
C. gracilis – MCZ A-5605 (female, 35.1 mm), Cameroon, Metet; MCZ A-35766 (male, 32.2 mm), Cameroon, Foulassi; MCZ A-136796 (male, 31.5 mm), UTA A44454 (female, 31.4 mm), Cameroon, Ntale Plateau, Southwest Province; MCZ A-137931 (male, 29.2 mm), MCZ A-137932 (male, 30.6 mm), MCZ A-137933 (male, 2–7.4 mm), MCZ A-137934 (male, 29.4 mm), MCZ A-137935 (female, 29.4 mm), MCZ A-137936 (male, 26.9 mm),Cameroon, Nkalakie, Center Province; MVZ 234675 (male, 33.8 mm), Cameroon, Fopouanga.
C. gratiosa – MHNG 1253.85 (male holotype, 22.7 mm), Cameroon, Ongot, Mt Kala, Center Province; BMNH 1947.2.3045 (?female, 29.9 mm), Equatorial Guinea, Benito River; FMNH 256784 (juvenile, 15.5 mm), FMNH 256785 (juvenile, 16.0 mm), respectively), Gabon; MCZ A3425 (female, 33.7 mm), MCZ A-5595 (male, 24.1 mm),Cameroon, Metet.
C. leucomystax – BMNH 1947.2.3044 (?female holotype, 31.0 mm), Equatorial Guinea, Benito River; MCZ A-2470 (male, 26.7 mm), Cameroon, Dja River; MCZ A-20972 (?female, 27.4 mm), Cameroon, Eschobi, Southwest Province; MCZ A-20973 (?female, 29.4), MCZ A-20974 (male, 24.9 mm), Cameroon, Makumunu, Southwest Province; MCZ A-21727 (male, 28.8 mm), MCZ A-21728 (juvenile, 23.0 mm), MCZ A-21729 (juvenile, 26.1 mm), MCZ A-21730 (male, 28.4 mm), Democratic Republic of Congo (DRC), Buta, Bas Velé; MCZ A-21731 (juvenile, 24.7 mm), DRC, Djamba; MCZ A-46622 (male, 30.3 mm), MCZ A-46623 (female, 35.1 mm), DRC, Katuka, Kivu Province; MCZ A-46624 (male, 27.1 mm), MCZ A-46625 (juvenile, 12.1 mm),DRC, Abyalose River, Kivu Province; MCZ A-46626 (female, 38.8 mm), MCZ A-46627 (female, 31.8 mm), MCZ A-46628 (female, 32.1 mm), DRC, Semliki River, Kivu Province; MCZ A-46629 (female, 32.0 mm), MCZ A-46630 (female, 32.3 mm), MCZ A-46631 (male, 27.3 mm), MCZ A-46632 (female, 38.1 mm), MCZ A-46633 (juvenile, 15.7 mm), DRC, Samboko River, Kivu Province; MCZ A-137923 (juvenile, 13.6 mm), Cameroon, Obang, Northwest Province; MCZ A-137929 (juvenile, 15.8 mm), MCZ A-137930 (juvenile, 18.0 mm), Cameroon, Nkalakie, Center Province; MVZ 234676 (female, 33.5 mm), MVZ 234677 (male, 27.3 mm), Cameroon, Fopouanga, West Province; USNM 563696 (male, 25.9 mm), USNM 563697 (?female, 30.1 mm), Cameroon, Ekomtolo, Littoral Province; USNM 563705 (?female, 28.8 mm), Cameroon, Yingui, Littoral Province; UTA A44585 (female, 28.6 mm), Cameroon, Ediensoa, Southwest Province; UTA A52321 (male, 30.5 mm), Cameroon, west of Nanga Eboko along the Tédé River, East Province.
C. melanogaster – MHNG 1253.86 (male holotype, 24.6 mm), Cameroon, Mwakoumel, Littoral Province; MCZ A-137905 (female, 29.8 mm), MCZ A-137906 (male, 28.5 mm), MCZ A-137907 (male, 26.6 mm), Cameroon, Nsoung, Littoral Province; USNM 563698 (?female, 27.5 mm), USNM 563699 (?female, 27.3 mm), USNM 563700 (?female, 23.7 mm), Cameroon, Nguéngué, Littoral Province.
C. nigromaculata – MHNG 1521.50 (male, 24.2 mm), Cameroon, Nkunjock.
C. occidentalis – FMNH 83121 (male paratype, 25.6 mm), FMNH 83122 (?immature male paratype, 23.3 mm), Sierra Leone, North Kambry; MVZ 244911 (female paratype, 34.8 mm), Ghana, Ankasa Conservation Area, Western Region.
C. oreas – MHNG 1253.87 (female holotype, 26.7 mm), MCZ A-137919 (juvenile, 16.4 mm), MCZ A-137920 (juvenile, 19.7 mm), MCZ A-137921 (juvenile, 16.4 mm), MCZ A-137922 (male, 22.3 mm), Cameroon, Bamboutos Mountains, West Province; MCZ A-137927 (female, 29.7 mm), MCZ A-137928 (male, 22.5 mm), Cameroon, Mount Oku, Northwest Province.
C. pulchra – ZMK R072173 (male holotype, 29.5 mm), Nigeria, Obudu Plateau, Ogoja Province; MCZ A-137916 (male, 29.4 mm), MCZ A-137917 (male, 31.0 mm), MCZ A-137918 (male, 25.8 mm), Cameroon, Bamboutos Mountains, West Province; MCZ A-137924 (juvenile, 18.2 mm), MCZ A-137925 (juvenile, 17.0 mm), Cameroon, Mount Oku, Northwest Province; MHNG 1521.58 (male, 26.6 mm), MHNG 1521.59 (male, 28.5 mm), Cameroon, Nsoung, Littoral Province.
C. schioetzi – ZMK R076631 (male paratype, 27.3 mm), Nigeria, Obudu Plateau; MCZ A-137911 (male, 23.2 mm), MCZ A-137912 (male, 24.2 mm), MCZ A-137913 (male, 24.4 mm), MCZ A-137914 (male, 24.2 mm), MCZ A-137915 (male, 24.4 mm), Cameroon, Mount Mbam, West Province; MCZ A-137926 (male, 27.0 mm), Cameroon, Mount Oku, Northwest Province.
C. trifasciata – MHNG 1253.88 (male holotype, 28.4 mm), Cameroon, Nsoung, Mt Manengouba, Littoral Province.
C. venusta – MHNG 1253.89 (male holotype, 29.3 mm), Cameroon, Fotabong, Southwest Province.